USING OTOLITH STRONTIUM ISOTOPES TO ELUCIDATE POPULATION STRUCTURE AND MOVEMENTS OF BERING CISCO (*COREGONUS LAURETTAE*)

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A

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ABSTRACT

Methods for stock discrimination and tracking the movements and distribution of fishes have often involved expensive field logistics, a problem compounded in remote regions such as Alaska. An alternative approach is to use the chemical signatures preserved in otoliths, or ear bones, of teleost fishes to discriminate stocks or to track the movement history of fish. Currently, a commercial fishery targeting the anadromous Bering cisco *Coregonus laurettae* is occurring in the Yukon River, Alaska. There are only three known Bering cisco spawning rivers worldwide, the Yukon, South Fork Kuskokwim (Kuskokwim), and Susitna rivers. Managers and researchers believed that two of the three spawning-river populations (Yukon and Kuskokwim rivers) were being harvested in the fishery, due to major coastal currents linking two of the spawning rivers' deltas. To determine the likelihood of a mixed-stock fishery, in Chapter 1, I used the strontium isotope signature ($^{87}Sr/^{86}Sr$) preserved in the freshwater portion of otoliths to establish a baseline for the three natal rivers. The baseline data set was composed of otoliths from spawning adult Bering cisco of known origin (n=82). Subsequently, the baseline was used to classify commercially harvested Bering cisco (n=139) and determine the stock composition of the fishery. Greater than 97% of the commercial samples were classified as Yukon River origin. However, 0.7%, and 1.4% of the commercial samples were classified as originating from Kuskokwim and Susitna rivers, respectively. In Chapter 2, I used the baseline data to classify Bering cisco from three coastal rearing areas (Alaska Arctic coast, n=49; Y-K Delta, n=70; and the Alaska Peninsula, n=8). More than 96% of the coastal rearing Bering cisco had $^{87}Sr/^{86}Sr$ signatures consistent with a Yukon River origin. These data demonstrate the wide-spread coastal distribution of Bering cisco, with some travelling >4,900 km between coastal rearing and spawning habitats. This approach illustrates that $^{87}Sr/^{86}Sr$ can determine the natal river of Bering cisco. Subsequently, this method can be used for stock discrimination and elucidating migration patterns for unknown origin Bering cisco.

TABLE OF CONTENTS

List of Figures

List of Tables

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GENERAL INTRODUCTION

Bering cisco *Coregonus laurettae* are important subsistence and commercial salmonids that bridge thousands of kilometers of coastal marine freshwater habitat over their life cycles. Similar to other coregonids in Alaska, Bering cisco is a data-limited species, which creates challenges for its conservation and management of anthropogenic influences along its coastal and freshwater migratory routes (e.g., fishing pressure, dam construction, etc.; Brönmark et al. 2013). Bering cisco spawn in the main stem of large rivers and rear in coastal marine waters (Alt 1973; Brown and Daum 2015). All three of the known spawning populations, the Yukon, South Fork Kuskokwim (Kuskokwim), and Susitna rivers, are in Alaska (Figure 1.1) and each of these natal rivers may be affected by human activities. Recently, a commercial fishery for the anadromous Bering cisco has emerged in the Yukon River Delta (Brown and Daum 2015), and a dam is planned for the Susitna River (Barringer 2013).

Prior to the start of this project, very little was known about population-specific migration and distribution patterns of Bering cisco. While the spawning areas have generally been defined (Alt 1973; ADF&G 1983; Brown and Daum 2015), the coastal distribution of each of these populations is speculated. Most Bering cisco are found in coastal areas of the Bering and Chukchi seas and are hypothesized to be of Yukon or Kuskokwim River origin (Craig 1989; Bickham et al. 1997), including those harvested in the Yukon River Delta commercial fishery. This hypothesis is based on the northward coastal currents in the eastern Bering Sea (Figure 1.1; Irvine et al. 2009; Sigler et al. 2011). Due to proximity, Susitna River Bering cisco are believed to primarily rear in Cook Inlet (Blackburn et al. 1981). Knowledge of stock structure and distribution of species are essentials for management decisions.

A recent tool that can be used to track the migration of fish is the strontium isotope composition ($^{87}Sr/^{86}Sr$) in a fish's otolith, or ear bone. $^{87}Sr/^{86}Sr$ signatures preserved in otoliths have been used to define distribution and migration patterns of diadromous fishes (Kennedy et al. 2002; Miller and Kent 2009; Barnett-Johnson et al. 2010). Otoliths are auditory structures composed of an aragonitic calcium carbonate lattice that accretes new material incrementally in concentric rings throughout the entire life of a fish (Campana 1999) and, in doing so, preserve the ambient water $^{87}Sr/^{86}Sr$ signature. Due to its conservative nature, $^{87}Sr/^{86}Sr$ has been successfully and broadly used in provenance research fields (Kennedy et al. 2002; Hobbs et al. 2005; Miller and Kent 2009; Brennan et al. 2015).

In Chapter 1, using $^{87}Sr/^{86}Sr$ from the fresh water portion of otoliths, I establish a baseline of natal stream isotope characteristics composed of samples from the three Bering cisco spawning rivers (Yukon, Kuskokwim, and Susitna rivers). Subsequently, I apportion Bering cisco caught in the commercial fishery to their natal river based on the $^{87}Sr/^{86}Sr$ composition of their otoliths. In doing so, I validate $^{87}Sr/^{86}Sr$ as a method for stock discrimination of Bering cisco in a mixed-stock fishery. In Chapter 2, I address the need for distribution data. Using the established baseline from Chapter 1, I determine the natal rivers of coastally rearing Bering cisco of unknown spawning origin (n=127). Subsequently, I determine the population-specific coastal distribution and migrations of these Bering cisco.

The use of strontium isotopes is becoming increasingly important in fisheries management. As global fish diversity declines, fisheries managers seek to maintain finer scales of species diversity amid climate change (Pereira et al. 2012; Christensen et al. 2014) and other human pressures (e.g., fishing, dams, etc.). $^{87}Sr/^{86}Sr$ can be a powerful tool for provenance and migration studies, specifically, when used to study facultative diadromous fishes whose groups derive from geochemically distinct rivers. This approach illustrates that strontium isotopes can be used to for provenance, investigating mixed-stock composition, and migration patterns of Bering cisco, but also has implications for other diadromous species such as Pacific salmon (*Oncorhynchus* spp.).

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CHAPTER 1:

Strontium isotope analyses ($^{87}Sr/^{86}Sr$) of otoliths from anadromous Bering cisco (*Coregonus lauretta*e) to determine stock composition[1]

ABSTRACT

A commercial fishery targeting the anadromous Bering cisco (*Coregonus laurettae*) is occurring in the Yukon River, Alaska, USA. All three of the known global spawning populations occur in Alaska. Managers believed that two of the three populations were being harvested in the fishery. To determine the likelihood of a mixed-stock fishery, we used $^{87}Sr/^{86}Sr$ values from the freshwater region of otoliths, from spawning adult Bering cisco of known origin (n=82), to create a baseline. A 10-fold cross-validated, quadratic discriminant function analysis (DFA) of the three baseline population $^{87}Sr/^{86}Sr$ values (Yukon River, n=27; South Fork Kuskokwim River [Kuskokwim River], n =25; and Susitna River, n=30) correctly reclassified 98.8% of the fish analysed. The baseline DFA model was then used to classify the $^{87}Sr/^{86}Sr$ values from a set of otoliths removed from commercially harvested Bering cisco (n=139). Using a posterior probability threshold of 90%, we found that >97% of the commercial samples were classified as originating from the Yukon River. The remainder of the commercial samples were classified as originating from the Kuskokwim River (0.7%) or from the Susitna River (1.5%). The presence of $^{87}Sr/^{86}Sr$ values consistent with the Susitna River discovered in the Yukon River baseline (n=1) and commercial samples (n=2) suggested either multiple isotope signatures within the Yukon River population or straying among populations. Strontium isotope data provide an effective tool to monitor the movements and stock composition of Bering cisco.

Key words: otolith; strontium isotopes, stock identification; fisheries management; *Coregonus laurettae*; Bering cisco

[1]Padilla, A. J., R. J. Brown, and M. J. Wooller. In revision. Strontium isotope analyses ($^{87}Sr/^{86}Sr$) of otoliths from anadromous Bering cisco (*Coregonus laurettae*) to determine stock composition. ICES Journal of Marine Science.

INTRODUCTION

Bering cisco (*Coregonus laurettae*) is an anadromous salmonid species endemic to Alaska. There are currently only three known spawning aggregations; one each in the Yukon River, the South Fork Kuskokwim River (Kuskokwim River), and Susitna River (Figure 1.1; ADF&G, 1983; Alt, 1973; Brown and Daum, 2015; McPhail and Lindsey, 1970). Currently, a fall commercial fishery is targeting Bering cisco in the Yukon River Delta. Managers and researchers are concerned that Bering cisco from the Kuskokwim River are being harvested in the Yukon River fishery, due to the northward flow of coastal currents near the fishery (Figure 1.1; Estensen *et al.*, 2012).To address this concern, we used strontium isotopes ($^{87}Sr/^{86}Sr$) to determine the likelihood of a mixed-stock commercial fishery.

Bering cisco spawn in freshwater rivers and rear in coastal marine waters. Mature adults return to natal rivers in summer and fall where they spawn in mid to late October (ADF&G, 1983; Alt, 1973; Brown and Daum, 2015). Adults may spawn more than once as evidenced by residual eggs (Brown *et al.*, 2012a). Few details about Bering cisco spawning behaviour and early life history are documented in the literature. However, other coregonid species broadcast eggs over gravel into the current where they drift downstream until they sink to the bottom and settle (McPhail and Lindsey, 1970; Næsje *et al.*, 1995). During the winter eggs remain in river gravel until the larvae hatch in April and May and are moved downstream during spring freshets or high flow periods (Næsje *et al.*, 1986, 1995). Bering cisco larvae are exposed to fresh water for a portion of their first summer as they out-migrate downriver toward coastal rearing areas. The distances from spawning grounds to the coast in the Yukon River are approximately 1,600 river kilometres (rkm; Brown and Daum , 2015), 840 rkm in the Kuskokwim River (Alt, 1973), and 120 rkm in the Susitna River (ADF&G, 1983). Juvenile Bering cisco are found in coastal estuaries and lagoons in Cook Inlet (McPhail, 1966) and in western Alaska from the Alaska Peninsula (Hildreth and Dion, 2006) to as far north as the Colville River (Figure 1.1; Bean, 1881; Bickham *et al.*, 1997; Craig, 1989). Most Bering cisco are found in coastal areas of the Bering and Chukchi seas and are hypothesized to be of Yukon or Kuskokwim River origin (Bickham *et al.*, 1997; Craig, 1989) as a result of the north-flowing ocean currents in the eastern Bering Sea (Figure 1.1; Irvine *et al.*, 2009; Sigler *et al.*, 2011). Rearing of Susitna River fish is believed to primarily occur in Cook Inlet (Blackburn *et al.*, 1981). Overwintering occurs in warmer brackish water and in river mouths (Craig, 1989, 1984) to avoid sub-zero marine temperatures (Sigler *et* *al*., 2011) considered lethal for fish in the family Salmonidae (Craig, 1989; DeVries and Cheng, 2005; Fletcher *et al*., 1988), such as Bering cisco. The minimum age of sexual maturity is 4 years old (Brown *et al*., 2012b) and once sexual maturity is reached, adults return to freshwater natal rivers to spawn.

Adult Bering cisco have been harvested in subsistence fisheries throughout their range in western Alaska (Georgette and Shiedt, 2005; Stickney, 1984). A commercial fishery for coregonid fishes (Coregoninae) developed in the lower Yukon River estuary in 2005 and has taken place during September and October of each year since. In 2006, Bering cisco became the targeted species (Bue *et al*., 2011). A harvest quota incrementally increased from 4,500 kg, approximately 10,000 fish, in 2005 to the 2014 quota of 25,000 Bering cisco (~11,300 kg). While the fishery was based on targeting the Yukon River population, there was concern the Kuskokwim River population was also being harvested due the northward flow of the Alaska coastal current (Estensen *et al*., 2013). The fishery is managed by the Alaska Department of Fish and Game, Division of Commercial Fisheries (ADF&G) in consultation with the U.S. Fish and Wildlife Service (USFWS). Fishing gear is currently limited to one gillnet up to 45.7 m in length and a maximum stretch-mesh size of 10.2 cm. Otolith samples collected from the harvested Bering cisco have been used to gain information regarding age composition of the population (Bue *et al*., 2011). Otoliths that had been aged were archived for future use. Based on age and gonadosomatic index (GSI) data, immature Bering cisco were found to be predominantly harvested in the fishery (Estensen *et al*., 2013). However, without stock identification methods in place for Bering cisco or Kuskokwim River population estimates, the extent of harvest on the neighbouring Kuskokwim River population has been a concern for fishery managers and researchers (Estensen *et al*., 2012).

Identifying separate populations or stocks in a mixed-stock fishery is essential for optimal sustainable harvest and the prevention of overexploitation of vulnerable stocks. One approach that has been successfully used to determine the natal river of fish species is analysing the strontium (Sr) isotope ratio ($^{87}Sr/^{86}Sr$ values) of fish otoliths (Barnett-Johnson *et al*., 2010; Feyrer *et al*., 2007; Hobbs *et al*., 2005, 2010; Ingram and Weber, 1999; Kennedy *et al*., 1997, 2002; Zimmerman *et al*., 2013). However, to our knowledge no published studies have further used baseline $^{87}Sr/^{86}Sr$ values to discriminate fish in a mixed-stock commercial fishery. Barnett-Johnson *et al*. (2010) underlined the need for reliable stock identification tools such as $^{87}Sr/^{86}Sr$, which requires $^{87}Sr/^{86}Sr$ baseline values for rivers. Once baseline $^{87}Sr/^{86}Sr$ values are established they may be sourced to track multiple populations within the same system (Barnett-Johnson *et al.*, 2010). Otolith $^{87}Sr/^{86}Sr$ values of fish stocks and individuals can be compared to data from a baseline map to determine the natal origin, distribution and behaviour of fish (Brennan *et al.*, 2015).

A major research milestone in terms of the development of $^{87}Sr/^{86}Sr$ as a tool to examine fish behaviour and migration in Alaska has been the development of a modelled strontium isotope map of water in Alaska (Bataille *et al.*, 2014; Brennan *et al.*, 2014). The main benefit of using $^{87}Sr/^{86}Sr$ values as a tracer is that no significant biological fractionation occurs between initial uptake over the gills and its subsequent incorporation into the otolith lattice (Blum *et al.*, 2000; Kennedy *et al.*, 2000; Koch *et al.*, 1992; Pouilly *et al.*, 2014). This means the $^{87}Sr/^{86}Sr$ values in freshwater portion of otoliths should reflect $^{87}Sr/^{86}Sr$ values in river water (Graustein, 1989; Kennedy *et al.*, 1997). However, it is worth noting some research indicates some biological fractionation of $^{87}Sr/^{86}Sr$ occurs (de Souza *et al.*, 2010; Halicz *et al.*, 2008). Nonetheless, $^{87}Sr/^{86}Sr$ remains an excellent proxy for provenance studies of diadromous fishes (Walther and Limburg, 2012)

Otoliths are paired structures that form part of the inner ear in teleost fishes. Accretion of biogenic calcium carbonate, usually the aragonite form, occurs throughout a fish's life and is deposited on a protein matrix (Radtke, 1984). The nature of the otolith matrix allows trace elements such as strontium, magnesium, and barium from ambient water to be incorporated into the otolith (Brennan *et al.*, 2015; Elsdon *et al.*, 2008; Kalish, 1989). Strontium, in particular, has the same charge and similar ionic radius as calcium and is readily substituted and randomly incorporated into otoliths (de Vries *et al.*, 2005; Degens *et al.*, 1969; Doubleday *et al.*, 2014). Strontium has four stable and naturally occurring isotopes: ^{88}Sr (82.59%), ^{86}Sr (9.86%), ^{87}Sr (7.0%), and ^{84}Sr (0.56%), of which only ^{87}Sr is radiogenic (Faure, 2001). Within a river drainage, ^{87}Sr varies based on the initial stock found in the surrounding geology as it is produced from the radioactive decay of ^{87}Rb (half-life of 48.8×10^9 years; Faure, 2001; Veizer, 1989). Thus, rocks derived from very old continental crust have had more time to accumulate ^{87}Sr than relatively younger (oceanic) crust (Faure, 2001; McDermott and Hawkesworth, 1990). Since the Yukon River flows through older geology (Archean), the riverine $^{87}Sr/^{86}Sr$ value (0.713285 ± 0.000028 2 standard errors (SE)) is distinct both from the Kuskokwim (0.709318 ± 0.000013 2

SE) and Susitna (0.708127 ± 0.000057 2 SE) rivers that flow through younger terrane groups (Cenozoic to Mesozoic) (Table 1.1; Bataille *et al*., 2014; Brennan *et al*., 2014). These discrete $^{87}Sr/^{86}Sr$ river values were used as a basis to address our objectives: 1) to determine if the $^{87}Sr/^{86}Sr$ values from the freshwater region of Bering cisco otoliths, from each of the three known spawning populations, are distinct, and if so, 2) to use these baseline data to determine the stock composition of the fishery.

METHODS

Sample collection

All otolith samples were provided from archived collections from ADF&G, Kuskokwim Native Association (KNA), and USFWS. Commercial samples have been collected annually from the lower Yukon River fishery since 2005 to provide age composition data to managers. Our baseline samples were collected opportunistically in conjunction with, though independent of, a genetic study on Bering cisco (see Schlei *et al*., 2013). All baseline samples were collected from adult Bering cisco at spawning locations or during spawning migrations. Baseline samples for the Yukon River (at Rampart Rapids, rkm 1,176) were collected in June and August 2010 (n=27), on 28 September 2010 (n=25) in the Kuskokwim River (rkm 944), and between 4–8 October in 2006-2011 (n=30) in the Susitna River near Montana Creek (rkm 124; Table 1.1). The commercially harvested samples were provided by ADF&G and were collected in three different areas in the Yukon River Delta, north mouth (n=49), south mouth (n=43), and Black River (n=48) from 9–13 September 2012 (Figure 1.1; Table 1.1). The 2012 commercial samples were selected for analysis based on the preliminary 2010–2012 genetic data of the commercial harvest indicating the greatest proportion of Kuskokwim River stocks in 2012 (Schlei *et al*., 2013).

Otolith preparation and analysis

Sagittal otoliths were thin sectioned in the transverse plane, mounted on petrographic microscope slides in Crystalbond™ 509, and were polished with 3 µm alumina slurry until the core was visible (Secor *et al*., 1992). In preparation for otolith chemistry analysis, individually mounted baseline samples were remounted on 1” x 3” microscope slides, with up to 30 otoliths per slide (Donohoe and Zimmerman, 2010). Otoliths were analysed using a Photon Machines Analyte G2 193 nm ArF excimer laser coupled to a Nu Plasma multi-collector inductively coupled plasma mass spectrometer (LA-MC-ICPMS) tuned to determine $^{87}Sr/^{86}Sr$ values. For the initial baseline samples, the laser was set to a pulse rate of 15 Hz with a 40 µm spot size, a speed of 5 µm/s, and 70% power output. For commercial samples, the laser was set with a 65 µm spot size and a rate of 5 µm/s. All strontium isotope data were corrected for mass bias interference of ^{87}Rb on ^{87}Sr following Woodhead *et al.* (2005). Two marine gastropod carbonate standards were analysed to track analytical accuracy and precision: an in-house deep-sea marine gastropod carbonate standard, collected in the Gulf of Mexico; and a *Neptunea* gastropod collected in the Chuckchi Sea (42 m, lat 66.6317°, long -168.8650°). We analysed each of the gastropods at the beginning, after every five otoliths, and at the end of each otolith slide. The deep-sea gastropod was determined with thermal ionization mass spectrometry (TIMS) (0.70919 ± 0.000008 2 SE; Miller and Kent, 2009) and the shallow, Arctic gastropod in solution with MC-ICPMS (see results). A mean gastropod $^{87}Sr/^{86}Sr$ value was calculated daily. As an additional measurement of instrument accuracy and precision, we measured $^{87}Sr/^{86}Sr$ values for a Batbjerg clinopyroxene standard, calibrated using TIMS, with each otolith slide. To ensure the freshwater $^{87}Sr/^{86}Sr$ values of each otolith was located, a transect (~1,000 µm in length) was selected perpendicular to, and encompassing, the first year of growth and core region (Figure 1.2). We measured $^{87}Sr/^{86}Sr$ values in the region of the otolith accreted in the natal river, prior to marine entrance, and just beyond the dark band associated with exogenous feeding (Marshall and Parker, 1982) and outside the influence of maternal marine influence in the core region (Bacon *et al.*, 2004; Barnett-Johnson *et al.*, 2005). All $^{87}Sr/^{86}Sr$ values were corrected for the difference between the daily gastropod $^{87}Sr/^{86}Sr$ value and the gastropod solution $^{87}Sr/^{86}Sr$ value (see results).

Data analysis

We used a quadratic discriminant function analysis (DFA) with 10-fold cross validation and 999 bootstrap iterations (Peters and Hothorn, 2013) to reclassify our baseline samples. The DFA assumes the number of groups is fixed (i.e., n=3, or no other populations; Venables and Ripley, 2002). The 10-fold cross validation method randomly divides the baseline $^{87}Sr/^{86}Sr$ values into to one of ten equal subsets (Hsu *et al.*, 2003; Peters and Hothorn, 2013). Sequentially, each subset is tested using the mean of the remaining subsets (Hsu *et al.*, 2003). The baseline DFA reassigns the baseline samples to one of the natal rivers and the cross-validation method provides a misclassification error. Since we were confident with the baseline model misclassification error (see results section), we used it to test the mixed-stock commercial samples. In the mixed-stock DFA, prior probabilities for each natal river, or group, were assumed to be equal (33%). For each sample, the mixed-stock DFA model produces a predicted group and a posterior probability of correct group membership assignment. Commercial samples with posterior probabilities >90% were retained for the final analysis. Welch's F-test was used for testing mean $^{87}Sr/^{86}Sr$ values between groups (Welch, 1951). All statistics were performed with R statistical computing software (R Core Team, 2014).

RESULTS

No significant difference in the mean $^{87}Sr/^{86}Sr$ values were detected between the deep sea and shallow marine gastropods, t (79)=0.14, α=0.05, p=0.89. In addition, the shallow marine gastropod standard analysed in solution with the MC-ICPMS produced a $^{87}Sr/^{86}Sr$ value of 0.709204 ± 0.000050 2 SD (M. Loewen, University of Oregon, personal communication), which is within analytical error of modern seawater (0.709182, Faure and Mensing, 2005). Subsequently, we used our shallow marine gastropod as the carbonate standard. Daily mean gastropod $^{87}Sr/^{86}Sr$ values (n=9) were calculated as 0.709278 ± 0.00024 2 SD. The Batbjerg clinopyroxene standard mean $^{87}Sr/^{86}Sr$ value (0.70444 ± 0.00038 2 SD, n=167) was within uncertainty of the accepted value (0.70447 ± 0.00002, Neumann, 2004).

Assumptions of homogeneity of variance and normality were not met for the Yukon or commercial samples. However, the DFA is robust against such violations of assumptions. Statistically significant differences were detected between the mean otolith $^{87}Sr/^{86}Sr$ values of the natal rivers, Welch's F-test (F(2,43)=215.2, p=0.00). The baseline DFA model resulted in 1.2% (n=1) misclassification or a total of 98.8% of samples being correctly reassigned to their respective natal rivers (Table 1.2). One Yukon River sample was incorrectly reassigned to the Susitna River (Figure 1.3; see discussion). Our baseline training DFA was subsequently used to classify the commercial samples. We found the three commercial sample sites to be similar (Welch's F-test, F(2,90)=1.38, p=0.26)) and subsequently pooled the data. Using a posterior probability threshold of 90%, 136 of the 139 commercial samples were retained for the final data set. Of those pooled commercial samples, 133 out of 136 were classified as Yukon River origin Bering cisco (97.8%; Figure 1.4). However, 0.7% (n=1) of the commercial samples were classified as Kuskokwim River origin, and 1.5% (n=2) were classified as Susitna River origin (Table 1.2; Figure 1.4).

DISCUSSION

Baseline river samples were successfully discriminated and reclassified into their respective spawning rivers solely using $^{87}Sr/^{86}Sr$ values. The baseline reclassification success of 98.8% was greater than chance alone (1/n groups), though from recent, and independent genetics results, the Yukon River fish were expected to dominate the sample size (Schlei *et al.*, 2013). The variability in the Yukon River samples may be indicative of the size and complexity of the watershed. Several minor tributaries feed into the Yukon River in the vicinity of the spawning area located in the Yukon Flats. The Porcupine River, the largest tributary of the Yukon River by drainage area with approximately 114,437 km^2, has a $^{87}Sr/^{86}Sr$ value of 0.71191 (Wadleigh *et al.*, 1985). Several of the Yukon River baseline otolith samples had similar $^{87}Sr/^{86}Sr$ values. In a recent radio telemetry study to determine Bering cisco spawning areas, Brown and Daum (2015) found 21% of tagged Bering cisco spawned downstream of the Porcupine River. We found that 25% of our Yukon baseline samples had similar $^{87}Sr/^{86}Sr$ values, which indicates that our samples are representative of the spawning population. One Yukon River sample was reclassified to the Susitna River. Likewise, two of the commercial samples were classified as Susitna River origin. This suggests that either multiple isotope signatures exist within the Yukon River population or some straying occurs among populations. However, since >4,800 km of coastline exists between the mouths of the Susitna and Yukon rivers, and an additional 1,600 km exists up the Yukon River to the spawning area (Brown and Daum, 2015), it seems unlikely that Susitna River fish are present in the fishery or among the Yukon River spawning population. Thus, we suggest a more plausible scenario is that multiple isotope signatures exist within the Yukon River spawning region due to the variation in the underlying geology influencing the tributaries or ground water. Recent isoscape models, using regional geology to predict $^{87}Sr/^{86}Sr$ values for Alaska (Bataille *et al.*, 2014), have shown areas upstream of the spawning area defined by Brown and Daum (2015) that may have $^{87}Sr/^{86}Sr$ values consistent with the Susitna River. Brown and Daum (2015) also found a few Bering cisco that remained upstream of Circle, Alaska, USA, and concluded this could be an indication of an additional spawning aggregation. However, further ground-truthing of strontium isoscape models in the Yukon River spawning area and exploring straying of the Susitna River population should be investigated prior to reaching a conclusion.

Our classification DFA model was applied to the 2012 Yukon River Delta commercial samples and classified 97.6% as Yukon River origin, 1.5% Susitna River origin, and 0.7% Kuskokwim River Bering cisco. Our $^{87}Sr/^{86}Sr$ results are consistent with results from genetic analyses of Bering cisco and indicate a small proportion (0-5%) of Kuskokwim Bering cisco were present in the 2012 fishery (Schlei *et al.*, 2013). This finding further validates $^{87}Sr/^{86}Sr$ as a method for determining the stock composition of the Bering cisco commercial fishery. The stock contribution of Kuskokwim River Bering cisco was negligible in 2012. Fishery managers have limited commercial harvest, even with increased quota requests from the fish buyer, due to uncertainty in the relative abundance and the unknown contribution of the Kuskokwim River population to the Yukon River fishery. Though we have shown the Yukon River dominates the commercial harvest, the size of the Yukon River population is still unknown. Our stock classification based on $^{87}Sr/^{86}Sr$ values can be used as an effective tool by managers to aid in monitoring of the stock composition of the fishery. The stock composition of the Yukon Delta may fluctuate inter-annually depending of the movement of coastal currents and salinity gradient along the coastline between the Yukon and Kuskokwim rivers. Stock identification is essential for the proper management of fish species, by allowing managers to monitor movements of harvested species and providing a sustainable harvest strategy while preventing overexploitation. Future monitoring of the fishery is important to evaluate any future changes to the stock composition until further determination of Kuskokwim fish movements and migrations, or relative abundance is clarified.

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TABLES

Table 1.1—List of sample locations, year, number of samples (n), and mean $^{87}Sr/^{86}Sr$ values for otoliths ($^{87}Sr/^{86}Sr_{otolith}$) and natal rivers ($^{87}Sr/^{86}Sr_{water}$).

Location	Year	n	$^{87}Sr/^{86}Sr_{otolith}$ mean	±2SD	$^{87}Sr/^{86}S_{water}$ mean[1]	±2SE[1]
Baseline	Total	82				
Yukon R.	2010	27	0.71253	0.00261	0.713285	0.000028
Kuskokwim R.	2010	25	0.70919	0.00057	0.709318	0.000013
Susitna R.	2006	1	0.70812	0.00036	0.708127	0.000057
	2009	10				
	2010	18				
	2011	1				
Commercial Fishery	Total	136				
North Mouth	2012	49	0.71259	0.00289		
South Mouth	2012	43	0.71296	0.00207		
Black River	2012	48	0.71302	0.00248		

[1] Source: Bataille et al., 2014

Table 1.2.—Commercial mixed-stock analysis results classified using a quadratic discriminant analysis.

	Predicted Group			
	Susitna R.	Kuskokwim R.	Yukon R.	Total
True Group				
North Mouth	1	1	44	46
South Mouth	0	0	42	42
Black River	1	0	47	48
Total	2	1	133	136

FIGURES

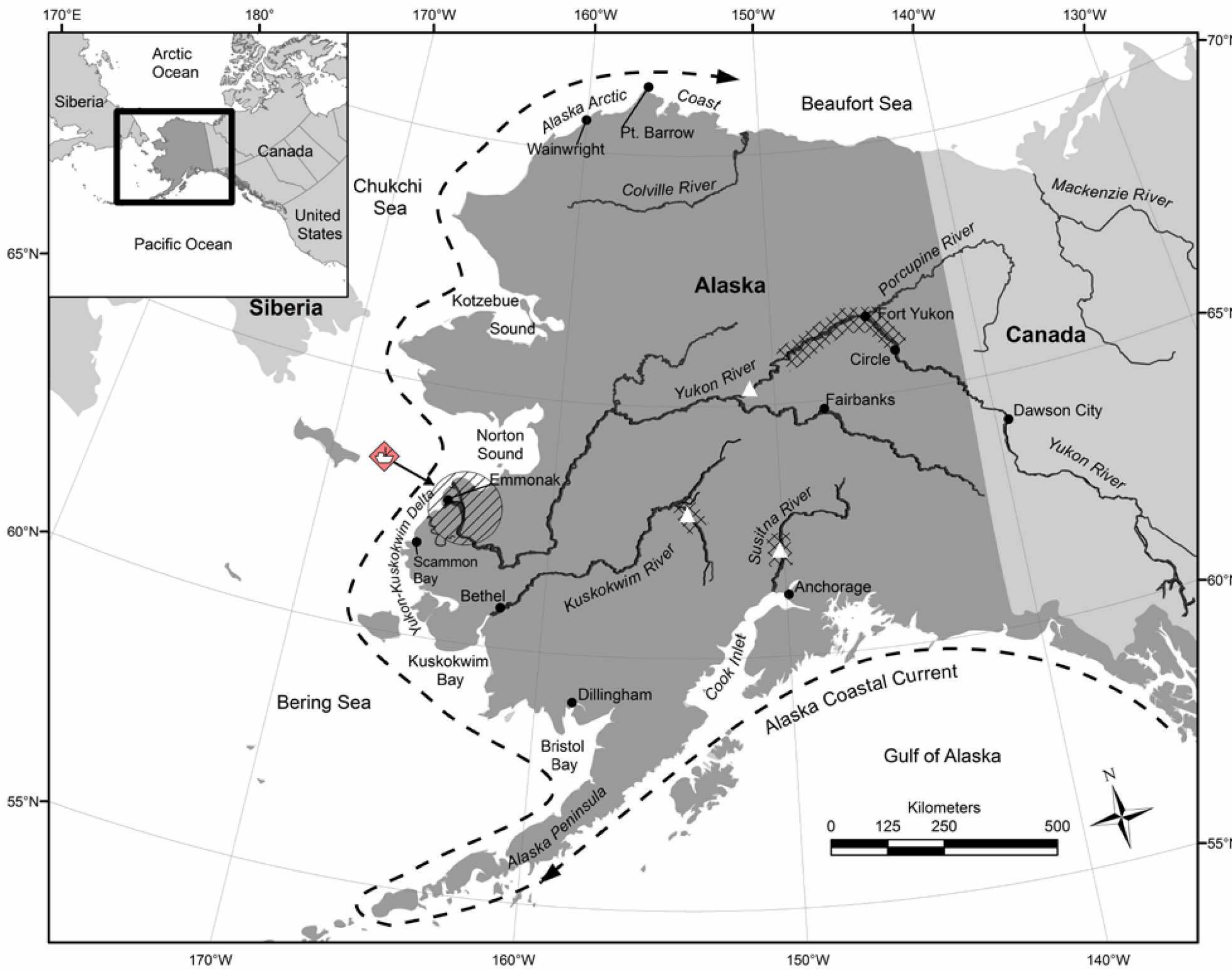

Figure 1.1—Map of spawning locations (cross-hatch) and baseline sampling locations (white triangles) in relationship to the commercial fishery (hatch circle) and north-flowing Alaska Coastal Current (dashed arrow).

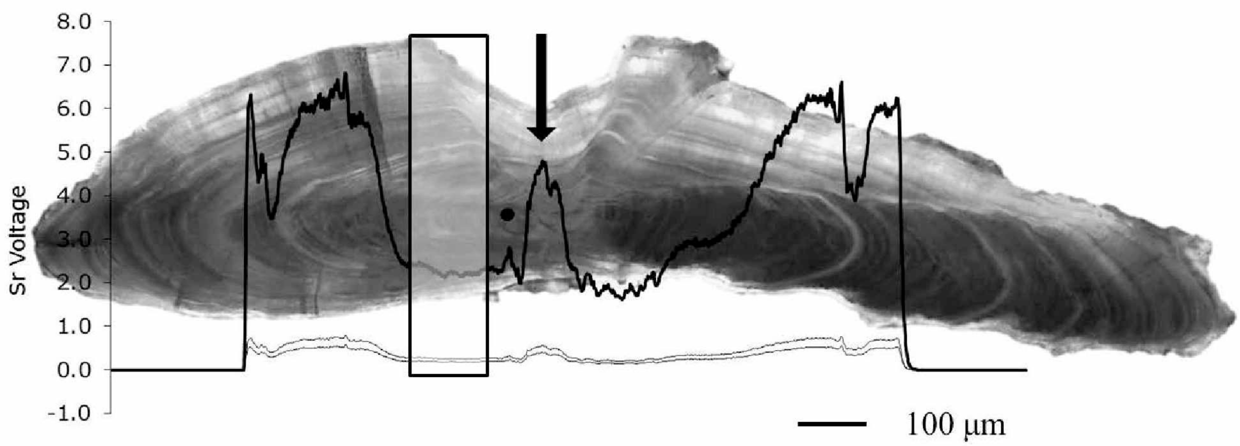

Figure 1.2—An example Bering cisco otolith sectioned in the transverse plane with strontium voltage (Sr voltage) shown, which was used to locate the portion of the otolith for determination of $^{87}Sr/^{86}Sr$ values and freshwater natal river (box). The exogenous feeding mark (circle) is proximal to the maternal marine strontium contribution in the core of the otolith (arrow).

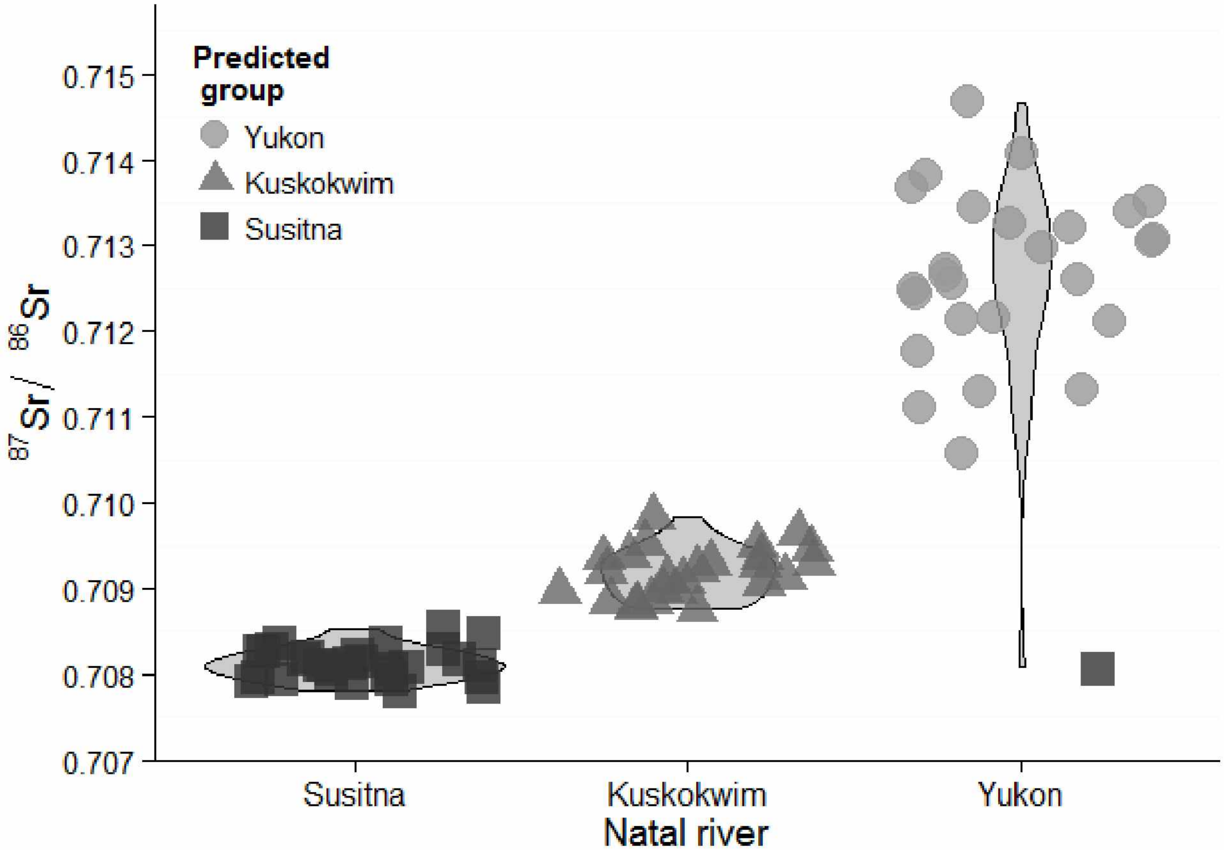

Figure 1.3—Baseline probability densities (grey polygon, i.e., violin plot) of each natal river and strontium isotope value ($^{87}Sr/^{86}Sr$) by sample. Using quadratic discriminant function analysis for classification, the natal river samples (x-axis) were reassigned into predicted groups (shapes) Data on the x-axis are jittered to show sample density. Note the one Yukon River sample predicted to be of Susitna River origin.

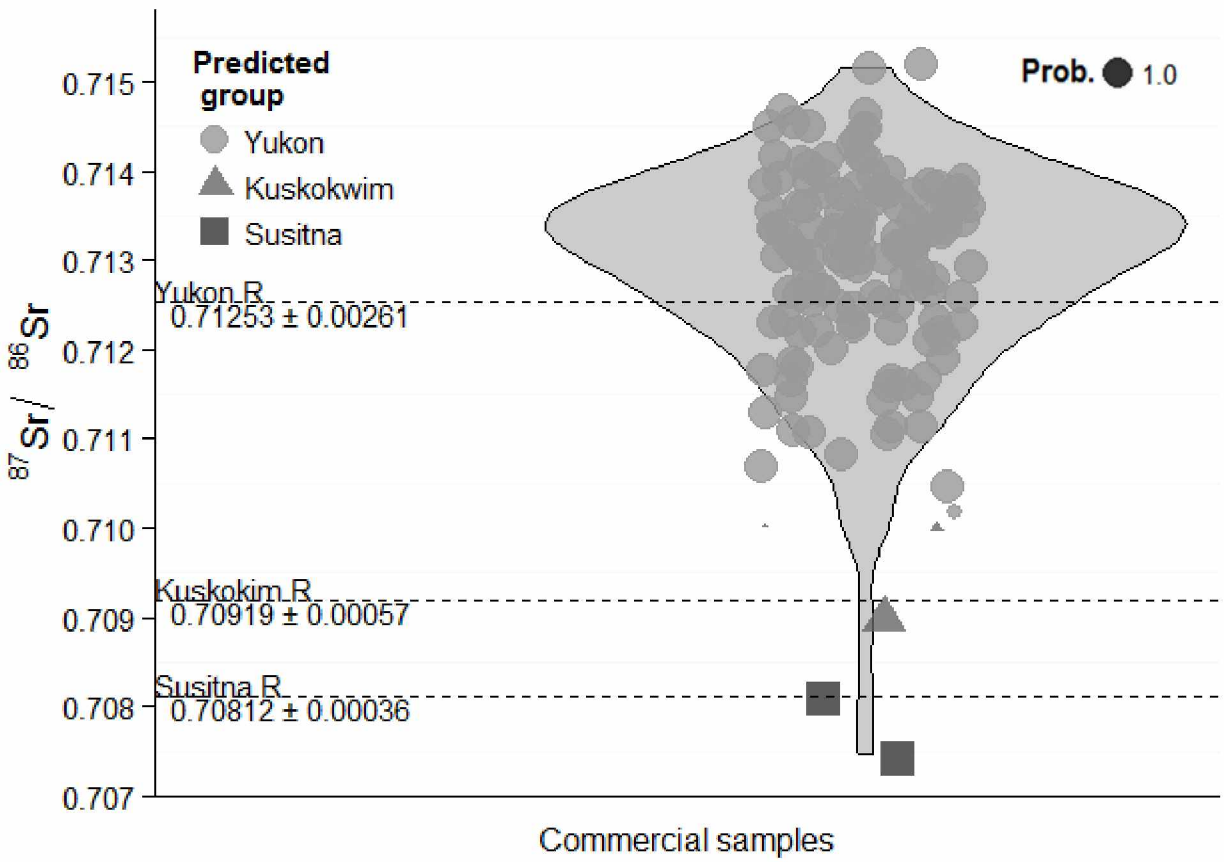

Figure 1.4—Commercial mixed-stock analysis. The probability density (grey polygon, i.e., violin plot) is shown surrounding the individual $^{87}Sr/^{86}Sr$ values and their respective predicted groups (shapes). The size of each shape (Prob.) is representative of each samples posterior probability (136 of 139 samples had posterior probabilities >90%). The mean baseline $^{87}Sr/^{86}Sr$ (dashed lines) and associated precision (±2 SD) are shown for comparison. Data on the x-axis are jittered to illustrate sample density.

CHAPTER 2:

Determining the movements and distribution of anadromous Bering cisco *Coregonus laurettae* using strontium isotope analyses of their otoliths[2]

ABSTRACT

Methods for tracking the movements and distribution of fishes have often involved expensive field logistics, which is compounded in remote regions such as Alaska. An alternative approach is to use the chemical signatures preserved in otoliths, or ear bones, of teleost fishes to track the movement history of fish. We used the strontium isotope signature ($^{87}Sr/^{86}Sr$ values) preserved in the freshwater portion of otoliths taken from Bering cisco *Coregonus laurettae* to identify their natal river of origin. Bering cisco spawn in freshwater rivers and rear in coastal marine waters. Only three known spawning rivers exist worldwide, the Yukon, South Fork Kuskokwim (Kuskokwim), and Susitna rivers. Rearing occurs commonly in coastal estuaries and lagoons on the Arctic coast of Alaska, the Yukon-Kuskokwim Delta (Y-K Delta), and rarely on the Alaska Peninsula. We compiled a set (n=127) of Bering cisco otoliths from fish caught in coastal habitats within each of these rearing areas. We measured the strontium isotope signatures from the freshwater portions of these otoliths and compared them to baseline signatures established for Bering cisco sampled from the known spawning locations in the Yukon, Kuskokwim, and Susitna rivers. We found that 96% of the specimens of unknown natal origin (Alaska Arctic coast, Y-K Delta, and Alaska Peninsula) had strontium isotope signatures that were consistent with a Yukon River origin. The dominance of Yukon River origin Bering cisco in all rearing groups suggests the Yukon River is considerably larger than the Kuskokwim or Susitna River populations. These data also demonstrate the wide-spread coastal distribution of Bering cisco, with some travelling >4,900 km between coastal rearing and spawning habitat. Our approach illustrates that strontium isotopes can be used to determine the natal river and migration behavior for fish of unknown origin.

Keyword: Bering cisco, *Coregonus laurettae*, movement, migration, otolith, provenance, strontium isotopes

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INTRODUCTION

Bering cisco *Coregonus laurettae* are anadromous salmonids with only three known spawning populations worldwide, one each in the Yukon, South Fork Kuskokwim (Kuskokwim) and Susitna rivers, in Alaska (Alt 1973; ADF&G 1983; Brown and Daum 2015). A commercial fishery for Bering cisco has recently developed with a current annual harvest quota of 25,000 fish (Padilla et al., in revision). Knowledge of Bering cisco distribution and migratory patterns are important for informed management decisions. We used strontium isotope analyses to elucidate the distribution and migration patterns of unknown origin Bering cisco captured in coastal rearing areas.

Bering cisco spawn in freshwater rivers and rear in coastal marine waters. Mature adults return to natal rivers in the summer and fall to spawn in mid to late October (Alt 1973; ADF&G 1983). The early life history and spawning behavior of Bering cisco is not well documented in the literature. However, other coregonid species broadcast their eggs over shallow gravel substrate where they settle to the bottom and remain for approximately 6–7 months (McPhail and Lindsey 1970; Næsje et al. 1986). Larvae hatch and emerge during spring freshets or floods (Næsje et al. 1995). Young Bering cisco are exposed to freshwater for up to 60 days as they migrate downstream to coastal rearing areas (Padilla, unpublished data). Bering cisco spawning occurs in the main stem of large rivers (Brown and Daum 2015). The distance from the spawning grounds in the Yukon River to the sea is approximately 1,600 river kilometers (rkm) (Brown and Daum 2015), 840 rkm in the Kuskokwim River (Alt 1973), and 120 rkm in the Susitna River (ADF&G 1983). Juvenile Bering cisco are broadly distributed in coastal estuaries and lagoons in western Alaska, from Kuskokwim Bay in the Yukon-Kuskokwim Delta, to Pt. Barrow and as far east as the Colville River Delta (Bickham et al. 1997) on the Alaska Arctic coast (Figure 2.1). Occurrences of Bering cisco have even been documented in Bristol Bay (Gilbert 1896; McPhail 1966) and on the Alaska Peninsula (Hildreth and Dion 2006; Anderson and Dion 2007, M. Plumb, US Fish and Wildlife Service [USFWS], unpublished data). Bering cisco have also been found in Cook Inlet in south central Alaska, near the Susitna River (McPhail 1966; Blackburn et al. 1981). No spawning migrations have been documented in Asia rivers flowing into the western Bering Sea or Arctic Ocean. However, two rearing Bering cisco were documented northwest of the Bering Strait in eastern Siberia, at the mouth of the Chegitun' River (Chereshnev 1984; Chereshnev et al. 2002). These are the only two individuals ever to be documented in Asia and most likely originated in Alaska (R. Brown, USFWS, personal communication). Overwintering occurs in warmer estuarine waters or near the mouths of rivers to avoid sub-zero temperatures in marine environments considered lethal for salmonids (Fletcher et al. 1988; Craig 1989; DeVries and Cheng 2005). The minimum age of sexual maturity is 4 years at a fork length (FL) of 31 cm (Brown et al. 2012). Once sexual maturity is reached Bering cisco return to spawn in their natal rivers. It is during this migration that they have been targeted in subsistence and commercial fisheries.

Arctic cisco *C. autumnalis* are also targeted in fisheries and are thought to exhibit similar life history patterns to Bering cisco. After McPhail (1966) confirmed Bering cisco as a separate species, using gill rakers, it was later reasserted using genetics (Bickham et al. 1997). Bering and Arctic ciscoe's coastal ranges overlap on the Alaska Arctic coast between Pt. Barrow and the Colville River Delta (Bickham et al. 1997). Arctic cisco spawn in the Mackenzie River, Canada. Researchers have found that age-0 Arctic cisco are advected westward with winds, greater than 5 cm/s, into the Colville River Delta, Alaska (Gallaway et al. 1983; Fechhelm et al. 2007). Young Arctic cisco rear for 5–6 years in the delta prior to returning to the Mackenzie River to spawn (Fechhelm et al. 2007). The Colville River Delta is a unique overwintering habitat for many other nearshore coregonid fishes (Coregoninae) such as least cisco *C. sardinella*, broad whitefish *C. nasus* and humpback whitefish *C. pidschian* (Craig 1989). As the extreme cold temperatures of winter descend on the Alaska Arctic coast, the reduced availability of overwintering habitat restricts Arctic cisco to the Colville River Delta (Craig 1989; Fechhelm et al. 2007). Soon after this transport mechanism for rearing Arctic cisco was understood, others realized it must also similarly occur for Bering cisco from the Yukon and Kuskokwim rivers (Craig 1989; Bickham et al. 1997).

The Alaska Coastal Current (ACC) is the major coastal current that is believed to concentrate the migration patterns of Bering cisco. Spring freshening of ice and snow melt and inputs of buoyant warm river discharge provide a seasonal migratory pathway for nearshore fishes (Craig 1984, 1989). Along the western Alaska coast, the mean flow of the ACC (approximately 14 cm/s near Barrow and 20–30 cm/s in the Bering Strait) is northerly and driven by a Pacific-Arctic Ocean sea level gradient, though strong southward winds in late fall and winter can cause current reversals through Bering Strait (Woodgate et al. 2005; Spall 2007).The ACC flows within reach of all three spawning rivers and known coastal rearing areas (Figure

2.1). Bering cisco are harvested through most of the region, though only a handful have previously been recorded from Bristol Bay (Gilbert 1896; McPhail 1966) or the Alaska Peninsula (Hildreth and Dion 2006, Anderson and Dion 2007, M. Plumb, unpublished data). As a subsistence resource they are targeted coastally in the fall and winter (Wolfe et al. 1984; Georgette and Shiedt 2005; Ray et al. 2010), and incidentally in freshwater during upriver summer spawning migrations (Brown et al. 2012). To a large degree, subsistence and commercial harvests of Bering cisco are conducted on coastal rearing immature fish prior to spawning migrations and have the potential for mixed-stock harvest (Padilla et al., in revision). Accordingly, it is important to gain knowledge of movements and migration patterns of Bering cisco to aid the management of each population.

Chemical signatures preserved in otoliths have been used to determine the movement and migration patterns of diadromous fishes (Kennedy et al. 2002; Brown et al. 2007; Miller and Kent 2009). Otoliths, or ear bones in bony fishes, are aragonitic auditory structures that accrete new material incrementally in concentric rings throughout the entire life of a fish (Campana 1999). The strontium isotope composition ($^{87}Sr/^{86}Sr$ values) of otoliths has been successfully used in the study of natal homing of a variety of fish species (Milton and Chenery 2003; Barnett-Johnson et al. 2008; Walther et al. 2008), juvenile nursery habitats (Hobbs et al. 2010), run timing (Miller and Kent 2009), movements and migrations (Kennedy et al. 2002; Milton and Chenery 2003; Brennan et al. 2015), and stock discrimination (Padilla et al., in revision). The main advantage to using $^{87}Sr/^{86}Sr$ values over elemental chemistry (e.g., Sr/Ca and Ba/Ca) is that no significant fractionation occurs during dietary or water uptake (Koch et al. 1992; Kennedy et al. 1997; Ingram and Weber 1999; Pouilly et al. 2014), it is not physiologically regulated (Blum et al. 2000; Kennedy et al. 2000), and it is geographically variable (Bataille et al. 2014, Brennan et al. 2015). Though, it should be noted recent work has suggested some biological fractionation in $^{87}Sr/^{86}Sr$ (Halicz et al. 2008; de Souza et al. 2010). Nonetheless, the use of strontium isotopes in fisheries management and provenance and migration studies can be a powerful tool (Walther and Limburg 2012), specifically, when used for fish species exhibiting facultative diadromy and whose groups derive from geochemically distinct rivers (Barnett-Johnson et al. 2008; Muhlfeld et al. 2012; Zimmerman et al. 2013). We measured the strontium isotope composition in the freshwater portion of otoliths from Bering cisco of unknown natal origin caught in three coastal locations (i.e., Alaska Arctic coast, Y-K Delta, and the Alaska Peninsula). Subsequently, we compared these signatures with our previously established baseline signatures measured from adult Bering cisco sampled from the three known spawning locations (Yukon, Kuskokwim and Susitna river; Padilla et al., in revision). Our overarching goal was to determine the natal origins of Bering cisco rearing in coastal habitats using strontium isotopes. Whereby, based on major coastal currents, we proposed three hypotheses: i) Bering cisco captured from the Alaska Arctic coast are of Yukon River origin, ii) samples from the Yukon-Kuskokwim Delta are a mixture of Yukon and Kuskokwim origin, and iii) those captured on the Alaska Peninsula are of Susitna River origin.

METHODS

Sample Collection

Archived otoliths from rearing Bering cisco from unknown natal origins were collected throughout the coastal waters of western Alaska, from the Alaska Peninsula to the Alaska Arctic coast (Figure 2.1). We grouped these capture locations into three regional rearing groups: the Alaska Arctic coast, Yukon-Kuskokwim Delta (Y-K Delta), and the Alaska Peninsula. The Alaska Arctic coast samples were collected from the Kungok (n=8), Colville (n=34), and Meade (n=7) rivers. Samples from the Y-K Delta included those collected from the Kun (n=52) and Black (n=18) rivers. On the Alaska Peninsula, samples were collected from Cold Bay (n=7) and the Ugashik River (n=1) (Table 2.1). A total of 127 samples from the three regions were analyzed.

Otolith preparation and chemical analysis

A sagittal otolith from each fish was thin-sectioned in the transverse plane, mounted on petrographic microscope slides using Crystalbond™ 509, and polished with 3 µm alumina slurry until the core was visible with transmitted light (Secor et al. 1992). Once prepared, otoliths were rinsed, dried and aged prior to being stored in slide boxes. In preparation for chemical analysis up to 50 otoliths were remounted on 1” x 3” microscope slides (Donohoe and Zimmerman 2010), ultra-sonicated for 5 minutes in Milli-Q© water, rinsed, and dried.

We used a Photon Machines G2 short pulse length ArF Excimer laser ablation (LA) coupled to a Nu Plasma multi-collector inductively coupled plasma mass spectrometer (MC-ICPMS) for *in situ* strontium isotope analyses at Oregon State University (OSU). An initial cleaning ablation (85 µm circle spot size and 20 µm/s) was performed over the surface of each otolith prior to analysis. After cleaning, the laser was set to a 65 µm diameter, a rate of 5 µm/s, and 70% laser energy. Counts were simultaneously measured at the Faraday cups for ^{83}Kr, ^{84}Sr, ^{85}Rb, ^{86}Sr, ^{87}Sr, ^{88}Sr with a machine integration time of 0.2 seconds. "On peak zero" methodology (Woodhead et al. 2005) was employed to remove any background interference of Kr and other monitored isotopes prior to ablation of each analysis. Mass bias interference of ^{87}Rb on ^{87}Sr was corrected by reference to an invariant $^{86}Sr/^{88}Sr$ ratio of 0.1194 and using exponential mass bias law (Woodhead et al. 2005). Analytical accuracy was determined using the analysis of $^{87}Sr/^{86}Sr$ values from an in-house modern marine gastropod carbonate standard (as in Padilla et al., in revision). We ran transects (250 µm) on the gastropod standard at the beginning, after the analysis of 5 otoliths, and end of each run, which were used to calculate daily mean $^{87}Sr/^{86}Sr$ values. The gastropod was also analysed in solution with the MC-ICPMS. All reported otolith $^{87}Sr/^{86}Sr$ values were corrected for the difference between the daily mean $^{87}Sr/^{86}Sr$ gastropod value and the gastropod solution value (see results).

Natal river determination

Bering cisco, like other coregonid fishes, spend several months in freshwater before the larvae hatch in the spring, emerge from the gravel, and migrate downriver toward coastal marine rearing areas (Næsje et al. 1986, 1995). To ensure the freshwater region was detected in the sample otoliths, transects encompassed the entire first year of growth, which included the core region, the freshwater residency period, and the transition to marine water. Each transect (ca. 1400 µm) was run dorsoventrally and perpendicular to the growth axis. We used the high variability of strontium concentration in otoliths, found in most diadromous fishes, to assist in defining freshwater residency (Zimmerman 2005). In anadromous fish otoliths, elevated levels of strontium can be found in the core region associated with maternal strontium, as well a sharp rise in the area associated with a fish's transition into a marine environment (Volk et al. 2000; Miller and Kent 2009). We defined the freshwater region as outside the influence of maternal marine strontium in the core (Bacon et al. 2004; Barnett-Johnson et al. 2005), distal to the dark band associated with exogenous feeding (Marshall and Parker 1982), yet prior to marine entrance. It is in this freshwater region we measured a minimum of 50 (ca. 50 µm transect) $^{87}Sr/^{86}Sr$ values to obtain a mean freshwater $^{87}Sr/^{86}Sr$ value for each otolith.

Data analysis

A mean freshwater $^{87}Sr/^{86}Sr$ value and an external precision (±2 standard deviations (SD) were calculated for each coastal rearing area (i.e., Alaska Arctic coast, Y-K Delta, and the Alaska Peninsula), and examined for homogeneity (using Bartlett's test), and normality (using Shapiro-Wilk test). We used Welch's F-test, robust against violations of variance homogeneity (Welch 1951), for comparisons of means.

We used a quadratic discriminant function analysis (DFA) to classify rearing Bering cisco from unknown origins (i.e., Alaska Arctic coast, Y-K Delta, and the Alaska Peninsula) using our previously established baseline DFA model of $^{87}Sr/^{86}Sr$ values in otoliths from known origin Bering cisco (i.e., Yukon, Kuskokwim and Susitna rivers) (Padilla et al., in revision). The mixed-stock (unknown origin) DFA prior probability of classification into each natal river was assumed to be equal (33.33%). For each sample, the mixed-stock DFA model classified each fish into one of the three natal river groups and produced a posterior probability of correct group membership. We set a 0.9 posterior probability threshold for group membership. All statistics were performed using R statistical computing software (R Core Team, 2014).

Migrations and rearing distributions were defined by interpolating the kilometers of coastline from coastal capture location and upstream river distance from predicted natal river spawning area. Rates of movement (10.5–17.2 km/day) are based on Arctic cisco on the Arctic coast (Fawcett et al. 1986, cited by Reist and Bond 1988) and are comparable to the mean current flow of the ACC near Barrow (14 km/day, Woodgate et al. 2005).

RESULTS

Daily mean gastropod $^{87}Sr/^{86}Sr$ values (n=10) were calculated to 0.709302 ± 0.000225 (2 SD). The gastropod standard has been analysed in solution with the MC-ICPMS and produced a $^{87}Sr/^{86}Sr$ value of 0.709204 ± 0.000050 (2 SD) (M. Loewen, University of Oregon, personal communication), which is within analytical error of modern seawater (0.709182 ± 0.000006 2 SD) (Faure and Mensing 2005).

Assumptions of homogeneity of variance and normality were not met for some data, however, statistics robust against such violations were used (e.g., DFA, Welch's F-test, DTK). Using our 0.9 posterior probability threshold, 126 of 127 samples were retained. Relative to our baseline DFA, 96% (n=121) of all the Bering cisco from unknown origins were classified as originating from the known spawning location in the Yukon River (Table 2.2; Figure 2.2). Of the remainder, 2.4% (n=3), and 1.6% (n=2), were classified as Kuskokwim or Susitna River origin, respectively. (Table 2.2; Figure 2.2). Of the Alaska Arctic coast group, 93.8% (n=45) were classified as originating in the Yukon River, 4.2% (n=2) in the Kuskokwim River, and 2.1% (n=1) in the Susitna River (Figure 2.3). All but two of the Y-K Delta group were classified as originating in the Yukon River (97.1%, n=68), and 1.4% (n=1) each in the Kuskokwim and Susitna rivers. The entire Alaska Peninsula group was classified as Yukon River origin (n=8, Table 2; Figure 2.3). Mean $^{87}Sr/^{86}Sr$ values (signatures) were similar between groups from the Alaska Arctic coast, Y-K Delta, and the Alaska Peninsula (Welch's F-test, $F_{(2,20)} = 0.42$, $p = 0.66$).

Having determined the likely natal streams of the coastal Bering cisco from previously unknown natal locations we then calculated that they were captured between 1,500 and 8,000 km from their classified natal river spawning areas (Table 3). Of the longest migrations, from spawning area to capture location, one Kuskokwim River fish was >4,900 km from its spawning area, which is approximately 840 rkm up the Kuskokwim River. One fish classified to be of Susitna River origin was captured in the Colville River approximately 8,000 km from its hatch location in the Susitna River (i.e., rkm 120) (however, see the discussion below regarding this particular fish). Yukon River Bering cisco were found throughout the geographic distribution with the greatest reliable migration distance calculated as ~4,800 km from the spawning grounds (~1,600 rkm from the Bering Sea). The Bering cisco of Yukon and Kuskokwim River origins travelled similar average distances, 3,652 and 3,669 km, respectively. Distinct are the two fish predicted as Susitna River origin, which traveled an average of 6,518 km (see discussion).

DISCUSSION

Our results show that samples of Bering cisco caught in the coastal rearing areas (i.e., the Alaska Arctic coast, Y-K Delta and Alaska Peninsula) are primarily of Yukon River origin. These results generally support the northward flow the ACC as a transport mechanism of Bering cisco northward, in western Alaska. However, the ACC does not explain the presence of Yukon River fish on the Alaska Peninsula.

Our first hypothesis was that the Yukon River population of Bering cisco was the source of Alaska Arctic coast samples of Bering cisco. Indeed, our results show that the majority of fish captured in the Alaska Arctic coast area are of Yukon River origin. A few Kuskokwim River fish, and one classified as Susitna River origin, were also identified in this area. Overall, our results are consistent with Bering cisco dispersal using major northward coastal currents, and are similar to wind-driven dispersal of age-0 Arctic cisco (Fechhelm et al. 2007).

Our second hypothesis was that there would be a mixed presence of Yukon and Kuskokwim origin Bering cisco in the Y-K Delta. As with the Alaska Arctic coast samples, we found the vast majority of fish were from the Yukon River population. The Y-K Delta is the closest area to the Yukon and Kuskokwim rivers. Assuming the Yukon River population is the largest, they may overshadow any presence of Kuskokwim River origin fish. However, we cannot be certain without further evidence, such as outmigration timing and population estimates of the Kuskokwim River population.

North of the Yukon River Delta, the available physical oceanographic data provide strong evidence to support the conjecture that larval and juvenile Bering cisco are transported northward via the ACC during the summer (Coachman 1986; Woodgate et al. 2005; Curchitser et al. 2013). Recent Chuckchi Sea drifter deployment data (10 m depth) confirm a general coastal warm (8–10°C), northward flow from the Bering Strait to Pt. Barrow from early August to September; thereafter, periods of cooler (2–6°C), southerly flow prevail until sea ice formation (Curchitser et al. 2013). The postulated emergence of Bering cisco larvae during spring freshets (Næsje et al. 1995) and their arrival into coastal waters into the Yukon River Delta (Martin et al. 1989) generally match the timing of the northward coastal movement of the ACC. Current reversals have been observed in the Bering Sea near Nunivak Island (Danielson et al. 2012) and in the Chuckchi Sea during the late fall (September–October, Woodgate et al. 2005). These periods of southerly ACC flow in the fall may encourage a general southerly migration of immature Bering cisco toward natal rivers, indications of which have been observed in fall subsistence catches in Kotzebue Sound (Georgette and Shiedt 2005). The synchronicity of currents and migrations between productive rearing habitat and spawning rivers may influence the success of ontogenetic stages in Bering cisco, specifically those from the Yukon River. For instance, Bering cisco may rear successfully north of the Bering Strait due to the lower relative abundance of piscivorous predators, such as Pacific salmon *Oncorhynchus* spp., and a relatively high abundance of prey items such as crustaceans (e.g., *Calanus* spp.), which are both characteristic of the Chukchi Sea (Sigler et al. 2011).

Lastly, we hypothesized that the Susitna River population was the source of the Bering cisco captured on the Alaska Peninsula. Although the Susitna River is the closest spawning river to the Alaska Peninsula and the ACC flows west from Cook Inlet toward the Alaska Peninsula we found no evidence of Susitna River Bering cisco. Numerous fisheries projects and nearshore surveys have been conducted throughout the Southeastern Bering Sea, Bristol Bay, and Alaska Peninsula, though just four discrete locations of captured Bering cisco exist (Gilbert 1896, McPhail 1966, Anderson and Dion 2007, M. Plumb, unpublished data). However, it is clear from our results that some portion of Yukon River Bering cisco migrate south against the flow of the major current. The driver behind this movement is not understood. Though, it is interesting to note this southern contingent, or group within a population exhibiting similar life history patterns, of Yukon River fish have a different migratory pattern. On a population level, the presence of contingents have been shown to increase the resiliency of the whole population, particularly when met with environmental perturbations (Secor and Kerr 2009; Walther and Limburg 2012).

Our results show two fish with Susitna River strontium isotope signatures, one each in the Alaska Arctic coast and Y-K Delta groups, but not the Alaska Peninsula group (Table 2.2). We propose that these fish instead are most likely from the Yukon River for three central reasons. Firstly, as presented in Padilla et al. (in revision), the presence of the Susitna River signature in the Yukon River baseline indicates the existence of multiple isotope signatures within the Bering cisco spawning area of the Yukon River. Recent isoscape mapping of Alaska (Bataille et al. 2014) shows areas with strontium isotope values consistent with the Susitna River isotopic signature, just distal to the known Yukon River spawning areas (Brown and Daum 2015) (Figure 2.4). Secondly, the geographical separation of the Susitna River and the Yukon River spawning grounds is greater than 6,500 km (Figure 2.1, Table 2.3). Furthermore, Bering cisco are rarely captured between southern Cook Inlet and Bristol Bay (Figure 2.1). Despite the annual presence of 18 state fisheries projects from southern Cook Inlet to Bristol Bay (Poetter and Nichols 2011; Jones et al. 2013; Wilburn and Murphy 2014) few data exist beyond those that we have presented (i.e., Cold Bay and Ugashik River). The most recent record was one Bering cisco caught near Dillingham (Bristol Bay) >45 years ago (McPhail 1966). Prior to this record, Gilbert (1896) recorded two juvenile Bering cisco near the mouth of the Nushagak and Naknek rivers in Bristol Bay. Lastly, Padilla et al. (in revision) conducted a mixed-stock analysis of the 2012 Yukon River Delta commercial fishery using the baseline $^{87}Sr/^{86}Sr$ values we have used here and found 1.5% of samples analysed had a Susitna River signature. However, they concluded those Bering cisco were most likely of Yukon River origin using some of the arguments we propose above. Thus, we believe our data support the hypothesis proposed by Padilla et al. (in revision) - but should be interpreted with caution until further research can clarify multiple isotope signatures in the Yukon River spawning area, or whether straying occurs between populations.

The methods we used may have misclassified some outlying fish as Susitna River origin. These outliers were assigned to one of the three natal groups based on probability, regardless of their true origin. Describing the movements of fish based on otolith chemistry is inherently limiting (Elsdon et al. 2008). Likewise, there are caveats for DFA classification methods (White and Ruttenberg 2007) that are sometimes used in the field of otolith chemistry (Feyrer et al. 2007; Walther and Thorrold 2009). In the DFA we assume only three spawning areas exist (i.e. one each in Yukon, Kuskokwim, and Susitna rivers), and no intra river spawning areas, which could have isotopic signatures similar to one of the other natal rivers. In our case, any secondary isotope signature within the Yukon River similar to that of the Susitna River would be misclassified as Susitna River origin. In addition, a DFA assumes multivariate normality and can be sensitive to small sample sizes (White and Ruttenberg 2007), but it has been shown to be robust (Solow 1990). It does not, however, assume homogeneity of covariance matrices, which is why we selected the quadratic model. One advantage to a DFA is the generated posterior probabilities for group membership. Very few otolith chemistry authors using DFA classification methods present posterior probabilities or, further yet, set a threshold as we presented here (Thorrold et al. 2001). Using posterior probabilities and setting a threshold is a conservative means of providing a measure of data confidence, particularly for data used for fisheries management decisions.

As previously proposed, Bering cisco were found to exhibit similar environmentally-driven distribution and migration patterns as the age-0 Arctic cisco from the Mackenzie River. However, we found they are also capable of moving against major coastal currents (Yukon River Bering cisco caught on the Alaska Peninsula). In contrast, Arctic and Bering ciscoes may have different migratory patterns that may be dependent on the seasonal availability of lagoons and estuaries used for overwintering habitat. Since the Alaska Arctic coast has few large estuaries or lagoons suitable for overwintering habitat (Craig 1984, 1989), Arctic cisco, advected from the Mackenzie River Delta, are limited to the Colville River Delta (Fechhelm et al. 2007). Whereas, the availability of overwintering habitat for Bering cisco, advected north toward the Chukchi Sea, is evident in their presence in lagoons and estuaries throughout Kotzebue and Norton sounds (McPhail 1966; Alt 1973; Georgette and Shiedt 2005).

Our results show surprisingly long distance rearing migrations, from hatch locations in the natal rivers to the sites of capture, considering the size of mature Bering cisco, 30–45 cm FL (Brown et al. 2012). In effect, these may be the longest known migrations of any coregonid and rival the migrations of their much larger relative, Pacific salmon. Other researchers have also documented long distance coregonid migrations using otolith chemistry. Brown et al. (2007) documented anadromous migrations of five Alaska coregonid fishes up to 2,000 km from the sea. Stephenson et al. (2005) found Mackenzie River inconnu *Stenodus leucichthys* had migrated approximately 1,800 km between fresh and marine waters. These long-distance migrations clearly have implications for energetics and may help explain why Bering cisco are targeted in fisheries due to their high fat content. Bering cisco are often prized for their high fat content by subsistence users (Georgette and Shiedt 2005; Brown and Daum 2015) and commercially caught fish are sold as a kosher delicacy in a New York City market (Fabricant 2008).

In conclusion, our study provides an alternative method to track movements and migration patterns of Bering cisco using the strontium isotope signature preserved in otoliths; it opens up avenues for the use of properly preserved collections of archived otoliths commonly in possession of management agencies and researchers.

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TABLES

Table 2.1—Sampling locations, and associated latitude and longitude in WGS 84 datum, capture year, number of samples (n), mean $^{87}Sr/^{86}Sr$ values ($^{87}Sr/^{86}Sr_{oto}$) and two standard deviations (±2 SD_{oto}). Note that only data with >0.9 posterior probability are presented for samples of the unknown origin group (126 of 127 samples analysed). The natal river strontium isotope compositions ($^{87}Sr/^{86}Sr_{water}$) with associated error (±2 SE_{water}) are sourced from Brennan et al. (2014). Each section (Baseline and Unknown Origin), in bold text, are organized by the furthermost north-easterly to south-easterly sampling locations. Samples of unknown origin are separated by geographic regional groups (italicized text), Alaska Arctic coast, Yukon Kuskokwim Delta, and Alaska Peninsula. Baseline data are modified from Padilla et al. (in revision).

Location	Latitude	Longitude	Year	n	$^{87}Sr/^{86}Sr_{oto}$ mean	±2SD_{oto}	$^{87}Sr/^{86}S_{water}$ mean	±2SE_{water}
			Baseline					
Yukon R.	65.33868	-151.0656	2010	27	0.71253	0.00261	0.713285	0.000028
Kuskokwim R.	62.86944	-154.0174	2010	25	0.70919	0.00057	0.709318	0.000013
Susitna R.	62.10549	-150.0859	2006	1	0.70812	0.00036	0.708127	0.000057
			2009	10				
			2010	18				
			2011	1				
			Total	82				
			Unknown Origin					
Alaska Arctic coast								
Colville River	70.35118	-151.0672	1990	33	0.71216	0.00256		
Meade River	70.87470	-155.9661	1990	7	0.71282	0.00452		
Kungok River	70.59290	-159.8895	2011	8	0.71262	0.00220		
Yukon-Kuskokwim Delta								
Black River	62.35996	-165.3503	2005	14	0.71234	0.00195		
			2006	4				
Kun River	61.81738	-165.3801	2005	10	0.71245	0.00304		
			2006	42				
Alaska Peninsula								
Ugashik River	57.56336	-156.9972	2004	1	0.71140			
Cold Bay	55.14667	-162.6332	2005	5	0.71289	0.00240		
			2006	2				
			Total	126				

Table 2.2.—Unknown origin coastal rearing group (capture location) composition by predicted group, or natal river.

	Predicted Group			
Capture location	Yukon R.	Kuskokwim R.	Susitna R.	Total
	Alaska Arctic Coast			
Colville River	31	1	1	33
Meade River	6	1	0	7
Kungok River	8	0	0	8
Subtotal	45	2	1	48
	Yukon Delta			
Black River	18	0	0	18
Kun River	50	1	1	52
Subtotal	68	1	1	70
	Alaska Peninsula			
Ugashik River	1	0	0	1
Cold Bay	7	0	0	7
Subtotal	8	0	0	8
Total	121	3	2	126

Table 2.3.—Estimated migration distances (km) and timing (days) from predicted spawning ground to capture location. Blank spaces indicate no samples were predicted from that sample location.

	Predicted Group					
	Yukon R.		Kuskokwim R.		Susitna R.[1]	
Location	Distance (km)	Days	Distance (km)	Days	Distance (km)	Days
Alaska Arctic Coast						
Colville River	4,849	282–462	4,911	286–468	8,170	475–78
Meade River	4,461	259–425	4,543	264–433		
Kungok River	4,445	258–423				
Yukon Delta						
Black River	1,669	97–159				
Kun River	1,729	101–165	1,553	90–148	4,865	283–463
Alaska Peninsula						
Ugashik River	3,691	215–352				
Cold Bay	4,537	264–432				

[1]See discussion for the Susitna River signature caught in the Colville River.

FIGURES

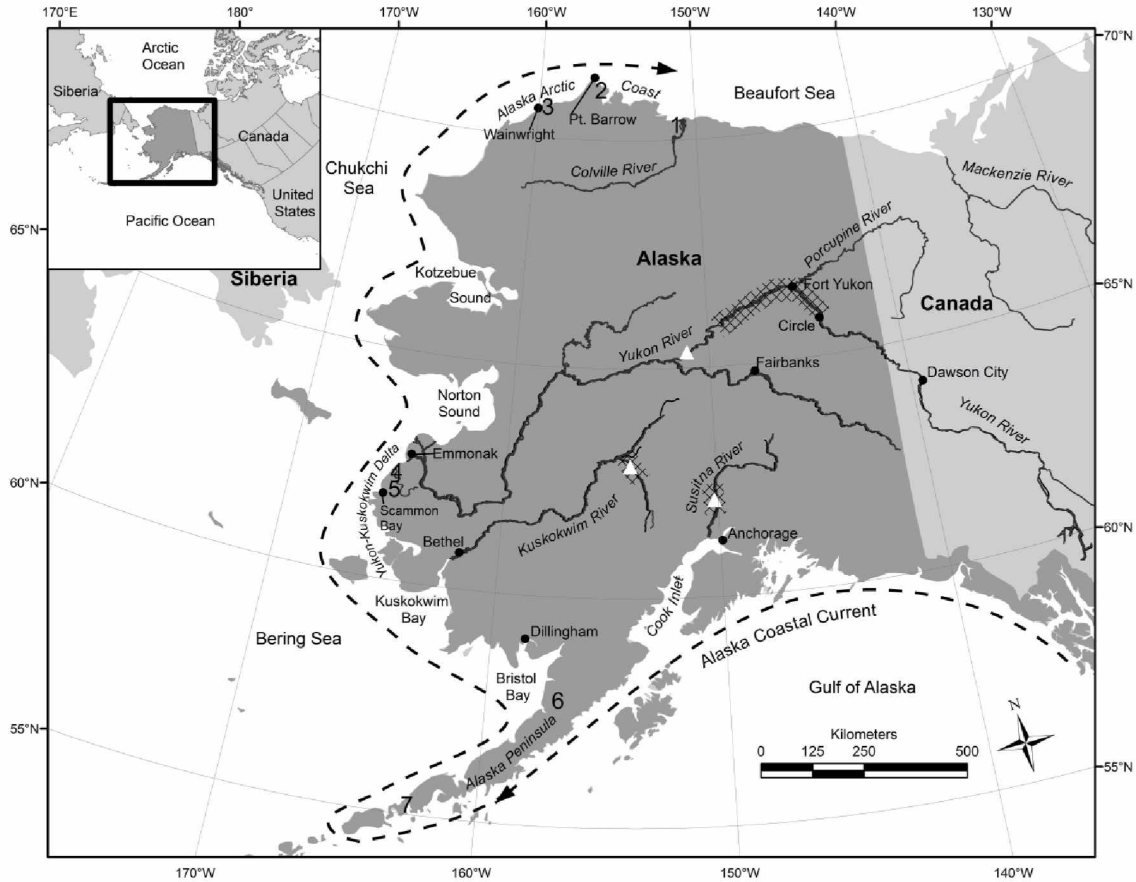

Figure 2.1—The known Bering cisco spawning areas (cross-hatch) and baseline sampling locations (white triangles). The approximate sampling locations of unknown origin Bering cisco are numbered. Alaska Arctic coast group includes: 1-Colville River, 2-Meade River, 3-Kungok River; Y-K Delta group: 4-Black River, 5-Kun River; and the Alaska Peninsula group: 6-Ugashik River, 7-Cold Bay. Also shown is the Alaska Coastal Current (dashed arrow).

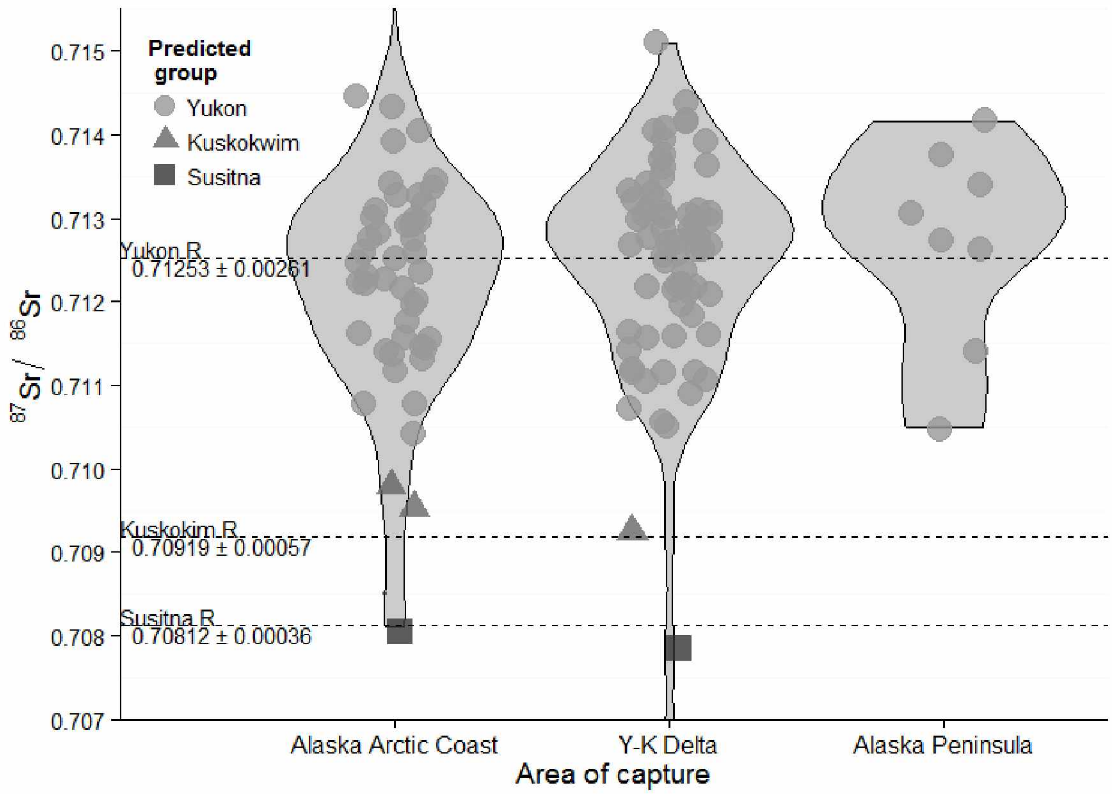

Figure 2.2.—The strontium isotope composition (^{87}Sr/^{86}Sr value) probability density for samples of unknown origin by regional group (Alaska Arctic coast, Yukon-Kuskokwim Delta (Y-K Delta), and Alaska Peninsula, and) on the x-axis. The x-axis data are jittered to show sample density. The shape of each sample is indicative of its predicted group. Note only samples that are >0.9 posterior probability are shown. The mean ^{87}Sr/^{86}Sr for each natal river is shown for comparison (dashed lines).

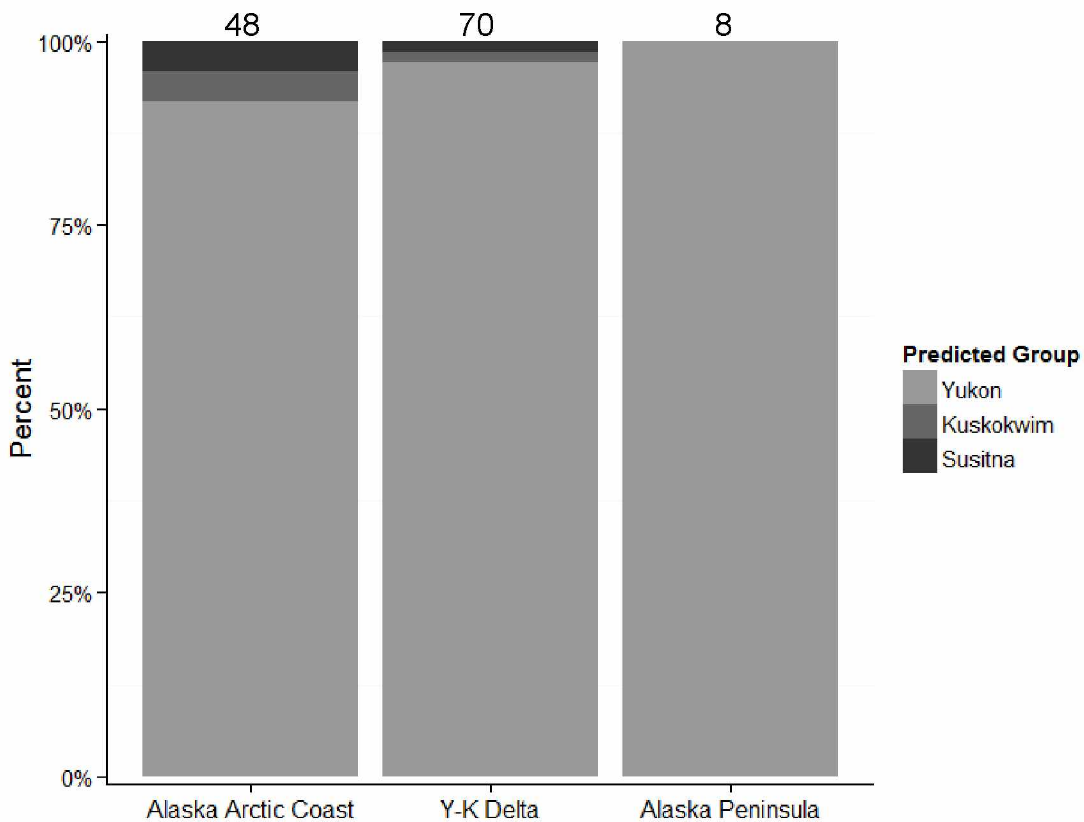

Figure 2.3—Mixed-stock analysis of the three regional rearing groups with samples of unknown origin and their predicted groups (variable greyscale colors). Sample sizes are over the bars of each group.

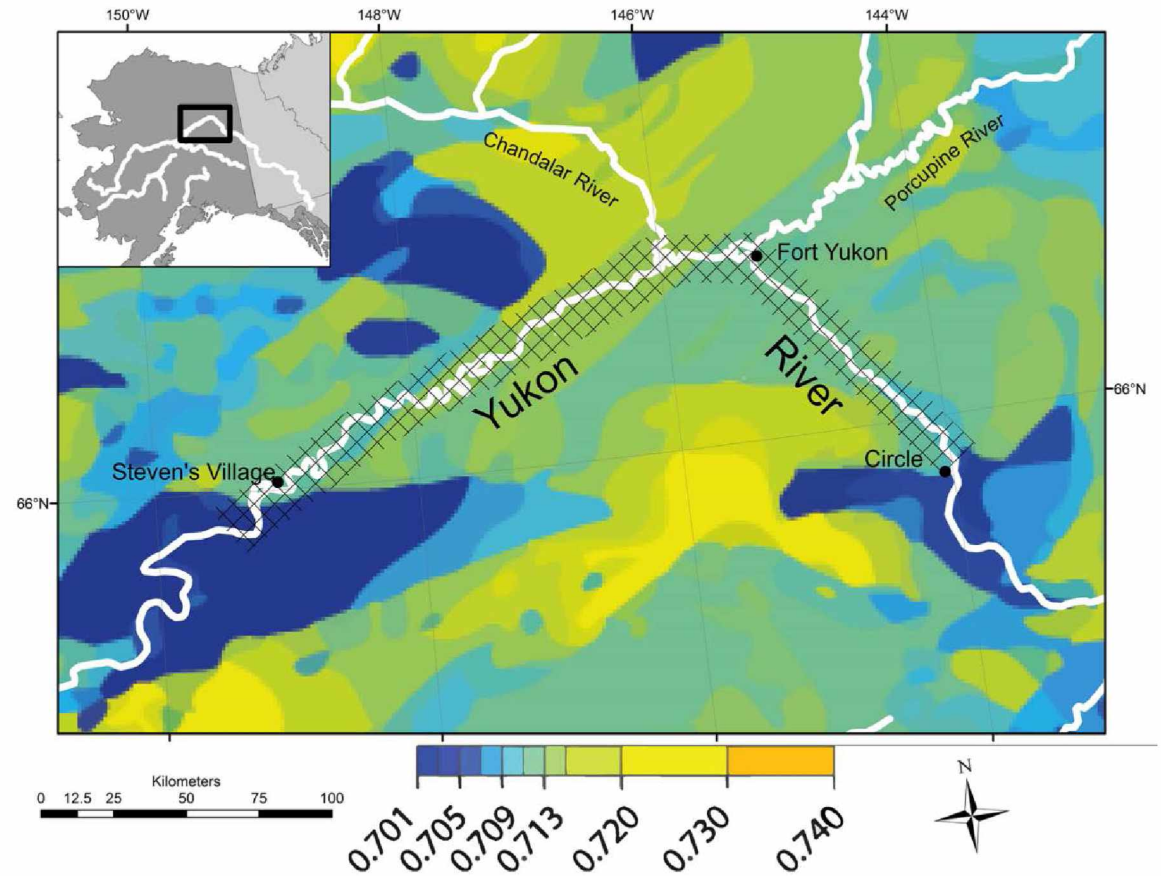

Figure 2.4—The strontium isotope composition of the environment (modified from Bataille et al. 2014) surrounding the Yukon River Bering cisco spawning area as defined by Brown and Daum (2015). This map shows areas of low $^{87}Sr/^{86}Sr$ (0.705–0.709) within the spawning area consistent with the Susitna River (0.70812).

GENERAL CONCLUSIONS

The diversity of Alaska's geography and variety of geologically distinct watersheds, coupled with an abundance of migratory species, makes strontium isotope analyses ($^{87}Sr/^{86}Sr$) an ideal tool for provenance studies throughout this state. In this thesis, I demonstrated that otolith $^{87}Sr/^{86}Sr$ can be successfully used to as a management tool to individually track and identify the natal origins of Bering cisco, an important subsistence and commercial fish. Furthermore, this thesis contributes to an understanding of the overall life history of Bering cisco and is an example of the use of strontium isotope analyses of otoliths as an environmental tracer and stock discrimination/composition tool.

To develop strontium isotope analyses of otoliths as a stock discrimination tool, and determine the extent of a mixed-stock fishery, I established a baseline composed of adult Bering cisco, from the three known spawning populations (Yukon, Kuskokwim and Susitna rivers). As the only variable, $^{87}Sr/^{86}Sr$ values were able to reclassify the baseline data back to natal origins with >98% accuracy. Therefore, using a quadratic discriminate function analysis, I was able to individually classify commercially caught Bering cisco, from an expected mixed-stock Lower Yukon River fishery, to one of the three natal rivers. Using $^{87}Sr/^{86}Sr$ values, the mixed-stock analysis (MSA) showed >97% were of Yukon River origin, indicating minimal contributions from the other populations to the fishery. These results compared very well to the genetics MSA for Bering cisco from the same year (Schlei et al. 2013), which further validates strontium isotope analyses of otoliths as a stock composition tool in the management of Bering cisco, and sets the stage for use with other geologically diverse anadromous fishes. Curiously, one Bering cisco from the Yukon River baseline and two commercial samples had a $^{87}Sr/^{86}Sr$ signature consistent with the Susitna River, to which I suggest the presence of multiple isotope signatures within the Yukon River population as the most plausible explanation. Though, straying of Susitna River fish cannot be ruled out without further clarification.

In addition to stock discrimination, by using my previously established baseline data set, I demonstrated the use of strontium isotope analyses of otoliths from Bering cisco as an environmental tracer. $^{87}Sr/^{86}Sr$ values were used to determine the natal origins and migration patterns of Bering cisco collected from three distinct coastal rearing areas, on the Alaska Arctic coast, Yukon-Kuskokwim Delta (Y-K Delta), and on the Alaska Peninsula. Based on the major coastal currents and geographical proximity, I hypothesized that i) Bering cisco caught rearing the Alaska Arctic coast were Yukon River origin; ii) the Y-K Delta were a mix of Yukon and Kuskokwim River origin, and iii) the Alaska Peninsula samples originated from the Susitna River. The $^{87}Sr/^{86}Sr$ MSA for these coastal rearing areas showed >95% of each group originated from the Yukon River. In addition, several interesting findings resulted: The dominance of Yukon River origin Bering cisco suggests they may be the most populous, or that the other populations maintain more localized migration patterns. Correspondingly, all of the Alaska Peninsula fish were classified as Yukon River origin, which is counter to major coastal currents, and my hypothesis of Susitna River origin. This finding alludes to the presence of two Yukon River contingents, or groups within the population exhibiting differing migratory patterns and habitat use. Finally, by measuring the coastline distance from coastal rearing areas to spawning areas, some Bering cisco had migrated >4,900 km one way, which is more than two times the longest previously known coregonid migrations (Alt 1977; Stephenson et al. 2005; Brown et al. 2007).

As previously proposed, Bering cisco were found to exhibit similar environmentally-driven distribution and migration patterns as the age-0 Arctic cisco from the Mackenzie River. However, I found they are also capable of moving against major coastal currents, as was observed with Yukon River origin Bering cisco caught on the Alaska Peninsula. This raises the questions: Why do some Yukon River Bering cisco migrate south toward the Alaska Peninsula?; Is the abundance of Yukon River fish in the coastal rearing areas overshadowing any presence of Kuskokwim or Susitna rivers populations or do these populations remain more local?- If the Kuskokwim and Susitna rivers' populations remain more local, what are differences between the biological or environmental drivers constraining locality, compared to those of the widely distributed Yukon River Bering cisco?; What are of short-term (lifetime) and long-term (evolutionary) implications of long-distance migrations on Bering cisco energetics? To begin answering some of these questions, population estimates are needed for the sustainable management of Bering cisco. In addition, to further define the coastal distributions for the Kuskokwim and Susitna rivers' populations, we might successively collect and analyze otolith $^{87}Sr/^{86}Sr$ from the mouths of spawning rivers out along coastal rearing areas.

The use of strontium isotopes in fisheries management, and provenance and migration studies can be a powerful tool, specifically when used with fish species exhibiting facultative diadromy or potadromy, and whose groups derive from geochemically distinct rivers. In these cases, strontium isotopes can provide fine scales of stock resolution (Barnett-Johnson et al. 2010). Used in combination with low spatial resolution genetics, otolith strontium isotopes can often provide finer resolution of stocks than genetics alone (see Feyrer et al. 2007; Barnett-Johnson et al. 2010; Zimmerman et al. 2013a), not only for Bering cisco but also for other salmonids. Pacific salmon *Oncorhynchus* spp. stocks are harvested throughout Alaska and the Pacific Northwest. Genetics baselines are established for some salmon species and are used to define many stocks, the stock identification resolution is often broad scale and cannot be further resolved to the fine-scale river or watershed level (Araujo et al. 2014). Some salmon species or stock do not have sufficient genetic variability (Araujo et al. 2014), or a baseline, as is the case for Yukon River coho salmon *O. kisutch* (Bonnie Borba, ADF&G, Fairbanks, personal communication). Depending on early life history patterns including the length of natal river residence, some river populations may be well suited for stock discrimination using strontium isotopes (Elsdon et al. 2008; Zimmerman et al. 2013b), or to determine movements as we have presented here. In Alaska, the recent advances in a strontium isoscape map (Bataille et al. 2014) will allow managers and researchers the ability to map out geologically discrete areas that may have potential for stock discrimination or movements of anadromous and freshwater fishes.

$^{87}Sr/^{86}Sr$ is a powerful tool for provenance and migration studies. The use of strontium isotopes in the management of anadromous fishes will become increasingly more important as global fish diversity declines and fisheries managers seek to maintain finer scales of species diversity; particularly amid global impacts, such as climate change and ocean acidification (Pereira et al. 2012; Christensen et al. 2014) and human influences.

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